DRYOPTERIS XLEEDSII AND ITS WESTERNMOST STATION[1]

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Dryopteris ×*leedsii* Wherry, Leeds' hybrid, is perhaps the most taxonomically confused of all eastern American woodferns. No other North American fern genus has received so much attention in recent years as *Dryopteris*, and the study of these plants reveals approximately three dozen taxa, of which two-thirds are sterile hybrids (Wagner, 1970). To the south and west the numbers of individuals and taxa become greatly diminished, as in the Gulf States and west of the Mississippi River. Thus, in Arkansas, woodferns are relatively rare. The occasion for this paper is the rediscovery of a long-problematic plant referred to as the "Palmer Dryopteris," found nearly fifty years ago and collected several times after that in a single locality in Arkansas. The study of this fern has forced us to review our knowledge of D. ×*leedsii* and related taxa, and we present the results of this review here.

As early as 1819, Thomas Nuttall (McKelvey, 1955) gave attention to the pteridophytes of Arkansas, which are currently being studied by one of us (Taylor). Of those who have made significant contributions to Arkansas pteridology in the past (Lesquereux, 1860; Harvey, 1881; Branner and Coville, 1891; Buchholz, 1924; Buchholz and Palmer, 1926; Scully, 1937, 1939; Moore, 1940a, b, 1941; and Demaree, 1943), no less than three, Palmer, Moore, and Demaree, have been concerned with the nature of the problematic *Dryopteris*. In spite of numerous field collections in Arkansas, especially since 1940, no new localities for the fern in question have been discovered, and the fern itself was not rediscovered at its original locality for almost 40 years.

A brief, published mention of the Palmer *Dryopteris* was given by Small (1938, p. 286). Because of its rather unusual nature, we expand its history here, based upon data from herbarium collections, and unpublished letters belonging to Delzie Demaree. Suffice it to say, not long after its original discovery, the fern attracted considerable attention from a number of individuals on the East Coast, including Small himself, W. R. Maxon, and E. T. Wherry. The main source of interest lay in the possibility that the plant might in fact represent a new and undescribed taxon. As will be shown, it really was a new taxon.

The plant was originally found by E. J. Palmer near Shirley, Arkansas, Van Buren County, on 30 March 1928 (*Palmer 33216*, NY, US) and identified as "*Dryopteris cristata* (L.) Gray." The specimens cited bear other identi-

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fications as "*D. celsa* E. T. W[herry]" and "*D. celsa* × *spinulosa* F. W. Crane." Both specimens have a ragged, coarsely lobed appearance, as if they had perhaps been grazed during growth or the plants had been damaged. Most of the later collections are more regular and more finely lobed. In 1932 there were collections by Delzie Demaree on 4 November (*Demaree 10039*, US—3 sheets). These were annotated by F. W. Crane (investigator on *Dryopteris*, especially comparative spore structure, during the 1950's) as "*D. celsa* × ?". On 3 November 1935, new collections were made at the same locality by Dwight M. Moore (*Moore 350441*, NY, US—2 sheets) and were annotated by Crane as "*D. celsa* × *marginalis*." A specimen of this collection in the Philadelphia Academy was annotated by Small as "*D. separabilis*."

William R. Maxon grew a living specimen of the Palmer *Dryopteris* at his home in Washington, D. C. from a rhizome sent to him by Demaree in 1932. We know (Maxon, *in litt.* 20 September 1933) that the fern survived at least through one summer, because he wrote to Demaree, "Your Arkansas *Dryopteris* has done remarkably well . . . ," and "it is an exceptionally attractive fern in cultivation." Evidently it did die, however, as there is no further mention of it, nor are there specimens from the cultivated plant in the National Herbarium. Maxon recognized that it was probably a new taxon. In a letter to Demaree (10 November 1932), Palmer wrote, "I have just had a letter from Dr. Maxon asking about a *Dryopteris* collected [at Shirley]. . . . He seems interested in it and thinks it is an undescribed species." Thus we have all the following interpretations that have been suggested for the Palmer *Dryopteris* through the years: *D. cristata*, *D. celsa*, *D. celsa* × *spinulosa*, *D. celsa* × ?, *D. celsa* × *marginalis*, *D. separabilis*, and an undescribed species.

In 1964, Wagner, in company with Delzie Demaree and Paul Redfearn, attempted to rediscover the Palmer *Dryopteris* but without success. It was not until August, 1974, that the plant was rediscovered. Taylor, in company with Demaree, found what may be at least a remnant of the original colony (or clone) from which the first specimens were taken.

The locality and habitat of the Palmer *Dryopteris* may be described as follows: Van Buren Co., ½ mi. SW of Shirley, NW ¼ of sect. 25, R13W, T12N, in moist, rocky woods below northeast-facing bluffs along the west bank of the Middle Fork of the Little Red River, on the Atoka Formation (shale and sandstone) of the Pennsylvanian Period, alt. 800-1000 ft. Conspicuous trees on the slope are *Acer saccharum*, *Carya* sp., *Carpinus caroliniana*, *Celtis occidentalis*, *Cornus florida*, *Fraxinus americana*, *Lindera benzoin*, *Quercus muehlenbergii*, and *Q. rubra*. Among the smaller woody plants are *Asimina triloba*, *Cercis canadensis*, *Corylus americana*, *Euonymus americana*, *Hydrangea arborescens*, *Smilax* sp., and *Toxicodendron radicans*. Students of the Ozarkian flora will recognize from these indicators the rich nature of the habitat. The soil here is very fertile, dark, sandy

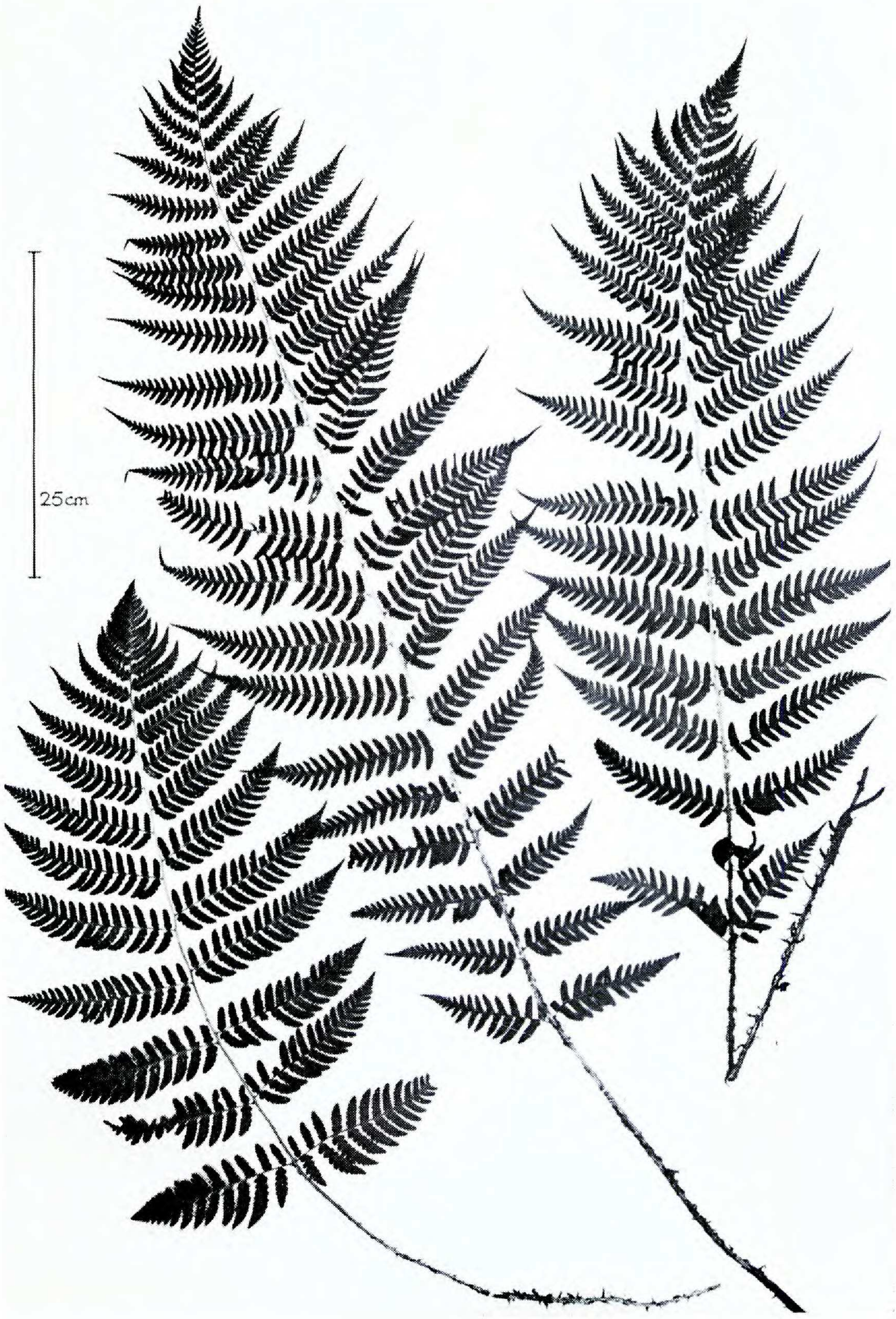
loam. Among the herbs are *Asarum canadense* and *Polymnia canadensis*. The associated ferns on the slope are *Adiantum pedatum*, *Polystichum acrostichoides*, and especially *Dryopteris marginalis*. The plants of the Palmer *Dryopteris* grow on the loose talus below the shale-sandstone cliffs. On the rocks directly associated with the colony are the mosses, *Anomodon attenuatus*, *A. rostratus*, and *Hedwigia ciliata*. The colony consists of 8-10 plants in an opening in the understory. The plants are concentrated in an area only about 4 feet in diameter in among the Atoka sandstone rubble. By October, all of the once stately fronds are lying down, criss-crossing each other.

VARIATION AND IDENTIFICATION OF THE PALMER DRYOPTERIS

The Palmer *Dryopteris* may be distinguished from the associated *D. marginalis* by its much larger fronds which taper basally, by the darker green color, thinner texture, and different position of the sori. Fertile fronds as tall as 45 inches, and sterile fronds as tall as 35 inches are represented in collections of *Wagner and Wagner 74164* (MICH). There is some evidence that it may reach even larger size, judging from a fragment of a frond from a Moore collection in 1935, deposited at the Philadelphia Academy. The distinctive color and texture of the fronds is due, apparently, to differences in the structure of the mesophyll. In *D. marginalis*, the color and rubbery texture appear to be due to the extremely large, stellate parenchyma cells of the mesophyll, whose almost worm-like arms result in extensive intercellular air-spaces. The Palmer *Dryopteris* is more like the usual condition in eastern American species, with smaller, more compact cells in the mesophyll. The position of the sori on the questionable plant is decidedly not marginal. Instead, the sori are located approximately one-third to one-half of the way to the costa.

The pinnules of different collections of the Palmer *Dryopteris* vary considerably in size and shape. Normally they are broadly adnate at their bases, but some are contracted, especially on very large fronds. The pinnules of the largest pinnae range from 0.4-0.9 cm. in maximum width and ca. 2-4 cm. in length. The most distinctive collections differ from the rest mainly in the structure of their pinnules. In the Philadelphia Academy, one of Moore's specimens taken in 1935 is represented only by a section of the blade which practically fills the herbarium sheet. The pinnules are

Figure 1. Comparison of two woodfern hybrids. Note relative petiole lengths, blade outlines, pinna numbers and shapes, and sizes of basal pinnae. LEFT: *Dryopteris* ×*neo-wherryi* (*D. goldiana* × *marginalis*), "Goldiana Valley," near Mountain Lake, Giles Co., Va., *Wagner and Wagner 70386* (MICH). CENTER: *D.* ×*leedsii* (*D. celsa* × *marginalis*), Shirley, Van Buren Co., Arkansas, *Wagner and Wagner 74164* (MICH). RIGHT: The same, *Redfearn 29403* (MICH).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strongly separated and are pinnatifid up to one-fourth of the distance to the costa. Also they are conspicuously contracted at their bases in the lower half of the pinnae, thus making the frond bipinnate-pinnatifid. The peculiar characteristics of this fragment are undoubtedly attributable to the very large size of the frond from which it came.

The 1928 Palmer specimens have some important similarities to the 1935 Moore collection. They both show evidence of damage (Fig. 2). They are extremely coarse, the ultimate segments broad and thick-textured, the margins jagged. Morphologically the specimens have the properties of "late fronds," of which similar examples have been detected in a number of *Dryopteris* species. Late fronds are formed as much as 1-3 months after the normal production of leaves, apparently as a result of injury and destruction of the fronds produced at the regular time. This phenomenon has not yet been examined in woodferns, but population samples of Christmas Fern (*Polystichum acrostichoides*) show that their late fronds have thicker texture, larger and fewer pinnae, and incised margins (Wagner, Farrar, and McAlpin, 1970, pp. 22-25). Perhaps the form of the Palmer specimens came about as a result of abnormal late growth following damage from a rock slide, lumbering or grazing in the area, or some other factor which injured or destroyed the normal fronds.

What is the identification of the Palmer *Dryopteris*? Now, as a result of bringing together all of the collections in the herbaria and our field studies, we are able to choose which of the previous suggestions is correct. First, we can eliminate, with fair assurance, several of the alternatives because our plant, in spite of its abundant production of sori and sporangia, is sterile. The spores are abortive, indicating that it is most probably a sterile hybrid. Thus, we can eliminate *D. celsa* and *D. cristata* as identifications. The majority of students of this plant have seen resemblances, however, to one of these species, namely *D. celsa* (W. Palmer) Small, a widespread but generally rare and sporadic eastern American species. The Palmer *Dryopteris* shows resemblances to *D. celsa* in such characters as blade outline, pinna structure, and position of the sori. Of the alternative hybrid combinations, we can eliminate *D. celsa* × *spinulosa* on the basis of frond texture and position of the sori, as well as the fact that *D. spinulosa* is absent at this locality. We can eliminate *D. celsa* × *intermedia* (= *D.* ×*separabilis* Small) on the basis of absence of epidermal glands and position of the sori, and, similarly, the absence of *D. intermedia* at the locality. This leaves us with *D. celsa* × *marginalis*, a striking hybrid, better known by its binomial *D.* ×*leedsii*. For several reasons this identification makes sense: (a) the frond shape and cutting, (b) the slightly "rubbery" texture, (c) the position of the sori, slightly above medial, and (d) the great abundance of *D. marginalis* at the locality. Comparison of the plant with collections from various localities of *D.* ×*leedsii* reveals that it is the same taxon. This, then, vastly increases the known range of this woodfern hybrid to the west.

Figure 2. Specimen from original E. J. Palmer collection, Van Buren Co., Arkansas, March, 1928, *Palmer 33216* (US).

The question immediately arises as to where *D. celsa* is in the locality. So far as we know—and we have made repeated searches for it there—the nearest locality for this parent is 75 miles away. The Log Fern, *D. celsa*, is very rare in the Midwest, and has usually been misidentified as *D. clintoniana* (D. C. Eaton) Dowell, the Northern Broad Swamp Fern. *Dryopteris clintoniana* occurs mainly in the Great Lakes area and New England and is not known south of Wisconsin glaciation. The following are specimens of *D. celsa* we have examined from the nearest localities: MISSOURI: Carter Co., Outlet of Blue Spring tributary to Big Barren Creek, 10 mi. NW of Bennett, *J. A. Steyermark 5333* (MO); the same, juvenile plants, *Steyermark 11858* (MO). ARKANSAS: Lawrence Co., "York Springs" (old York Estate), approximately 3½ mi. S of Imboden [*fide* Demaree], 24 May 1925, *B. C. Marshall 9* (US). Polk Co., Ouachita Mts., N side of Missouri Mt., valley of Big Fork Creek, ca. 1 mi. W of Big Fork, elev. ca. 800 ft., dense, deciduous, rich woods at base of steep, rocky, north-facing slope, along small streams, 12 October 1952, *D. M. Moore, A. McWilliam,* and *H. H. Iltis 52040* (US).

SYNTHESIS OF OUR KNOWLEDGE OF D ×LEEDSII

The history of this taxon is a good example of the gradual increase of understanding that has characterized so many of the hybrid ferns in recent years. Apparently, the first discovery of *D. ×leedsii* was that of the Palmer *Dryopteris* in 1928, but it remained a mystery until the present. In 1931, Arthur N. Leeds discovered a fine population of it near the banks of the Susquehanna River in Maryland, where it was growing with *D. marginalis*. He and all subsequent workers until 1965 interpreted the plant as the hybrid of Goldie's Fern, *D. goldiana* (Hook.) A. Gray, and Marginal Wood Fern, *D. marginalis* (L.) A. Gray. Small (1938, p. 286) confused the Palmer *Dryopteris* with his new species from the Great Dismal Swamp, Virginia, *D. separabilis*, and postulated that it had its ancestry in the mountains and spread to the lowlands, now remaining "in only two outposts, retreats as it were, one the Dismal Swamp, the other the hills of Arkansas." Wherry (1942) decided to give the Susquehanna plant a name, and he honored the discoverer of that colony by naming it for him, *D. ×leedsii*. The full latin diagnosis is as follows: "*Planta hybrida inter Dryopterem goldianam et D. marginalem, folius sempervirentibus, soris medialibus.*" This misinterpretation of its origin continued through 1962, when Stanley Walker (1962b) of the University of Liverpool, published his very important cytological studies of the Susquehanna population. Of the cytotypes found there, he interpreted a fertile tetraploid ("*D. wherryi* F. W. Crane") as the possible form of *D. ×leedsii* in which the chromosome number had doubled, but he conceded that there were problems with this interpretation. Accordingly, in 1963, Wherry and Wagner revisited the Susquehanna locality and discovered that what Crane had named "*D. wherryi*" was, in fact, *D. celsa*. This explained why typical *D. ×leedsii* had been found by Walker to be a triploid, as *D.*

Figure 3. Very broad form of *D.* ×*leedsii* from the type locality, Harford Co., Md., October, 1963, *Wagner and Wherry 63172* (MICH).

celsa is a tetraploid and *D. marginalis*, the other associate, is a diploid. Thus, *D.* ×*leedsii* proved not to be *D. goldiana* × *marginalis*, and this fact was revealed in a publication based on studies in the vicinity of Rochester, N. Y. (Wagner and Wagner, 1965). The following year, the distinctions between *D. celsa* × *marginalis* and *D. goldiana* × *marginalis* were delineated and the latter was designated as *D.* ×*neo-wherryi* (Wagner and Wagner, 1966). One of the curious by-products of this study was the discovery that the spores of *D.* ×*leedsii*, in spite of their high level of abortion, are remarkably capable of germination, with over one-third of a sample actually forming prothallia (Whittier and Wagner, 1971). In the meantime, the new discoveries about *D.* ×*leedsii* encouraged field explorations for it. Not only was it found in 1964 in the vicinity of Rochester, N. Y., but also near Thurmont, Md. the same year. In 1970, a colony was discovered by Wherry and Wagner near Morgantown, Pa. Finally, the Palmer *Dryopteris* was rediscovered after nearly forty years by Taylor, thus making it possible to bring together the whole picture.

We now know of six localities in four states for this taxon, with the Arkansas locality well over 800 miles disjunct. Three of these localities, those marked with asterisks in the enumeration given here, are herewith reported for the first time: NEW YORK — Monroe Co., "Riga Swamp," 1 mi. E of Genesee Co. line along route NY 33A (Mr. Pym's property), low swampy woods, 18 April 1964, *W. H. Wagner* and *F. S. Wagner 64010* (MICH). Genesee Co., Bergen Twp., Pocock Entrance to Bergen Swamp, low, swampy woods, 19 April 1964, *Wagner* and *Wagner 64018* (MICH). PENNSYLVANIA — *Berks Co., 0.5 mi. NE Joanna Furnace (ca. 4 mi. NE Morgantown), on rocky seepage slope in woods above road, 5 December 1970, *W. Wagner* and *E. T. Wherry 70519* (MICH). MARYLAND — *Frederick Co., 1.4 mi. W of Thurmont, just S of road along Hunting Creek (just inside recreation area) on rocky seepage slopes, 10 March 1964, *W. Wagner, C. V. Morton,* and *D. B. Lellinger 64005* (MICH). Harford Co., N bank of Susquehanna River near Rock Run, rocky slope 2 mi. N of Lapidum, 26 October 1963, *W. Wagner* and *E. T. Wherry 63172*, TYPE LOCALITY (MICH). ARKANSAS — *Van Buren Co., near Shirley, numerous collections cited above in text, plus *Carl Taylor* and *Jerry Taylor 2597* (SIU), *Paul L. Redfearn* and *Alice Redfearn 29403* (SMS), *Wagner* and *Wagner 74164* (MICH).

We can summarize our knowledge of *D.* ×*leedsii* in the following way: An interspecific hybrid woodfern growing usually with both parents, *D. celsa* and *D. marginalis*, rarely with only one parent, in rich, damp soil of low, swampy forests or on rocky, usually springy slopes. A magnificent, tall, and decorative fern combining the characters of its parents, and differing from *D. goldiana* × *marginalis* (= *D.* ×*neo-wherryi*) in: (1) being more evergreen; (2) having somewhat more numerous pinnae, these (3) more triangular, and (4) more reduced at the blade base, and (5) having more medial sori. The habitat is somewhat more moist for *D.* ×*leedsii*.

Cytogenetically it is triploid, rather than diploid (Wagner and Wagner 1966, pp. 133-136, figs. 5-7). The plant is rare and known at present from only a few localities in the region New York to Maryland, with an isolated locality in Arkansas. Reproduction is apparently entirely by rhizome proliferation, although some evidence exists for spore dispersal since, as previously mentioned, an unusually large number of otherwise abortive spores are capable of germination.

The Arkansas locality of *D.* ×*leedsii* has special interest because it is so separated from the rest of the known stations far to the east, because one of the parents is missing at the locality, and because what is apparently the same colony has persisted there for nearly a half-century. Perhaps at this, or one of the other localities, *D.* ×*leedsii* may double its chromosome complement, thus becoming a sexually reproducing fern. Its cytogenetic constitution may be expressed, according to our present knowledge, as GLM, where G = *D. goldiana* genome, L = *D. ludoviciana* genome, and M = *D. marginalis* genome (the evidence for this interpretation is summarized in Wagner, 1970). If automatic chromosome doubling occurred this would presumably form an allohexaploid with the cytogenetic constitution of GGLLMM with normal pairing and spore production.

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